

Using opportunistic photo-identifications to detect a population decline of killer whales (*Orcinus orca*) in British and Irish waters

SUZANNE BECK¹, ANDREW D. FOOTE², SANDRA KÖTTER³, OLIVIA HARRIES³, LAURA MANDLEBERG³, PETER T. STEVICK³, PÁDRAIG WHOOLEY⁴ AND JOHN W. DURBAN⁵

¹Marine Biodiversity Research Group, Galway—Mayo Institute of Technology Dublin Road, Galway, Ireland, ²Center for GeoGenetics, Natural History Museum of Denmark, University of Copenhagen, Øster Voldgade 5-7, DK-1350 Copenhagen K, Denmark, ³Hebridean Whale and Dolphin Trust, 28 Main Street, Tobermory, Isle of Mull, PA75 6NU, UK, ⁴Irish Whale and Dolphin Group, Dereen, Rossmore, Clonakilty, Co. Cork, Ireland, ⁵Marine Mammal and Turtle Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 8901 La Jolla Shores Drive, La Jolla, CA 92037, USA

An assemblage of killer whales that has been sighted in waters off the west coast of the British Isles and Ireland has previously been shown to be isolated from other North Atlantic killer whale communities based on association patterns. By applying a Bayesian formulation of the Jolly–Seber mark-recapture model to the photo-identification data compiled from opportunistic photographic encounters with this population of killer whales, we show that such sparse and opportunistically-collected data can still be valuable in estimating population dynamics of small, wide-ranging groups. Good quality photo-identification data was collected from 32 encounters over 19 years. Despite a cumulative total of 77 identifications from these encounters, just ten individuals were identified and the remaining 67 identifications were re-sights of these ten animals. There was no detected recruitment through births during the study and, as a result, the population appears to be in a slight decline. The demography of the population was highly skewed towards older individuals and had an unusually high ratio of adult males, and we suggest that demographic stochasticity due to a small population size may be further impacting the population growth rate. We recommend that this population be managed as a separate conservation unit from neighbouring killer whale populations.

Keywords: killer whale, *Orcinus orca*, mark-recapture, population decline, citizen science

Submitted 19 November 2012; accepted 17 July 2013

INTRODUCTION

Effective conservation management to ensure the viability of marine top predators requires the delineation of population units and the monitoring of population dynamics within these units (Taylor, 1997). The status of killer whales in the UK and adjacent waters is not well known (Joint Nature Conservation Committee, 2007). They are listed on the Scottish Biodiversity List and with other sea mammals as a priority group of species on the latest UK Biodiversity Action Plan, which states that there is no evidence for ‘moderate or marked decline’. However, these conclusions are based on sparse, mostly non-effort-based sightings data that do not include individual identification. In recent decades, north-east Atlantic killer whale populations have been subject to a number of anthropogenic threats, including bioaccumulation of organic pollutants (Law *et al.*, 1997; McHugh *et al.*, 2007; Wolkers *et al.*, 2007); prey depletion (Cañadas & de Stephanis, 2006); and exploitation by both lethal and live-capture fisheries (Øien, 1988; Sigurjónsson & Leatherwood, 1988). In locations where long-term studies of

photographically-identified individuals facilitate long-term monitoring of discrete communities, such factors have been shown to have population-level impacts (Olesiuk *et al.*, 1990; Matkin *et al.*, 2008, 2012; Ford *et al.*, 2010; Poncelet *et al.*, 2010).

Recent work using photo-identification data and genetic analysis of tissue samples has provided the first information on population structuring in the north-east Atlantic, and suggests that killer whales sighted in UK or Irish waters belonged to several distinct populations including highly divergent matrilineal lineages (Foote *et al.*, 2009, 2010, 2011). Photo-identification data and field observations indicate that relatively large numbers of individuals are associated with the north-east Atlantic mackerel stock in the North Sea during the autumn (Luque *et al.*, 2006; Foote *et al.*, 2010). Photo-identification data have also shown that approximately 50 individuals are highly site-faithful and return each year during the spring and summer months to the Northern Isles (Shetland and Orkney) and the north-east of Scotland, and are known to feed on grey and harbour seals and occasionally eider ducks (Foote *et al.*, 2010; Beck *et al.*, 2012). These individuals are linked through association patterns to a large number (>200) of individuals photo-identified off the east coast of Iceland (Foote *et al.*, 2010; Beck *et al.*, 2012), and so appear to be a part of a larger population.

Corresponding author:
O. Harries
Email: biodiversityofficer@hwdt.org

In contrast, previous analysis of data on individual identifications of an assemblage of killer whales found off the west coast of Scotland, Ireland and Wales, suggested it was isolated from other local killer whale groups based on association patterns (Foote *et al.*, 2010). These individuals have not been identified in any of the 108 photo-identification encounters recorded from the Northern Isles and the north-east of Scotland between 2005 and 2011, or matched with the large photo-identification catalogues from Iceland and Norway (Foote *et al.*, 2010; Foote, unpublished data). Re-sightings of individuals from this group indicate this community's range includes the west coast of Scotland, waters around Ireland and the waters off the south-west coast of Wales, and that they are site faithful, with all individuals having been seen off the west coast of Scotland in at least two different years (Foote *et al.*, 2010). All individuals within this population share the same 'sloping' eye patch shape, which is relatively distinct from the eye patch pattern of most other individuals photographed around Scotland and other parts of the north-east Atlantic. This also suggests a degree of reproductive isolation, in addition to social isolation.

Here, we further analyse photo-identification data collected between 1992 and 2011 around the west coast of the UK and Ireland by the Hebridean Whale and Dolphin Trust (HWDT) and the Irish Whale and Dolphin Group (IWDG) during dedicated boat-based cetacean surveys on the SV 'Silurian' and collected opportunistically from the public and local whale watching communities through the establishment of sightings networks.

MATERIALS AND METHODS

A pool of photographs taken between 1992 and 2011 in UK and Irish waters was used for this study. All of the photographs were taken on an opportunistic basis without any special protocol. Photographs were taken by trained field workers on HWDT surveys, and by members of the public. Photographs were graded on photographic quality and the distinctiveness of the individual. Photographs in which the fin and saddle filled less than 10% of the photograph, were not in focus, were poorly lit or in which the animal was not parallel to the camera were excluded. The best photograph of each individual from each encounter was then selected.

Approximately 60% of opportunistic encounters resulted in suitable quality photographs for use in photo-identification studies of all or most individuals present. Each photographed whale was given a rating (M) of how well marked they were, ranging from 0 to 2 following previous studies (Poncelet *et al.*, 2010). Individuals were classified as: 'well-marked' ($M = 2$) if they were sufficiently distinctive for re-identification without the risk of false positives or negatives (Figure 1A), based on the presence of symmetric long-lasting markings such as fin-nicks, or collapsed dorsal fin; $M = 1$ if they had markings that could fade over the long-term or were asymmetrical, such as scars or pigmentation on the saddle patch (see Similä & Lindblom, 1993); or unmarked ($M = 0$) if there were no clearly visible nicks or scars (Figure 1B).

For some photographed individuals we were able to establish stage of maturity and sex class; this was partially achieved using body size. The presence of secondary sexual characteristics could be used to identify adult males. Individuals that were full-grown adult males when first observed were assumed to be ≥ 18 years old at that date. Some female-sized individuals did not develop secondary sexual characteristics from when they were first photographed, and if sufficient time had passed when last observed, they were confirmed as adult females rather than sub-adult males. Individuals that were adult female size when first observed and did not subsequently grow were assumed to be ≥ 14 years old at that date.

A discovery curve was plotted to assess how the number of individuals identified photographically related to the amount of data collected. To assess population dynamics more formally we fitted the Jolly-Seber mark-recapture model to the annual photo-identification histories to estimate both additions and losses to the population (Seber, 1982). Specifically, we used a Bayesian formulation of the model (Royle & Dorazio, 2008; Fearnbach *et al.*, 2012) to incorporate inherent uncertainty resulting from the sparse photo-identification dataset, and communicate this uncertainty in the form of direct probability distributions. As all individuals were identifiable when only high-quality photographs were used, we included all individuals in the analysis. We assigned flat (uniform) prior distributions between 0 and 1 to each of the annual probabilities of identification, survival and entry into the population, and derived statistics for annual abundance, N_t , number of deaths, D_t (or permanent emigrants), and recruits, R_t , from the model parameters; the population



Fig. 1. (A) Individual with a significant natural mark (' M ' quality value = 2; photograph N. Van Geel); (B) individual without any significant natural mark (' M ' quality value = 0; photograph G. Leaper).

growth rate $\lambda_t = R_t/D_t$ was estimated as the ratio of births to deaths in each year, t .

The model was fitted using Markov Chain Monte Carlo (MCMC) sampling using WinBUGS software (Lunn *et al.*, 2000), after augmenting the data for the ten observed individuals with up to ten possible unobserved individuals (Royle & Dorazio, 2008). Inference was based on 10,000 repeated draws from the posterior distribution of each model parameter conditional on the observed data, following MCMC convergence (Brooks & Gelman, 1998), and the estimates of parameter values across MCMC iterations was used to estimate the probability that the population growth rate, λ_t , in each year was less than one (i.e. declining). We employed the same MCMC simulation approach to generate predictive observations from the model to examine goodness-of-fit (Gelman *et al.*, 1996). We calculated the summed absolute discrepancies to the model for both the predicted and observed data (e.g. Durban *et al.*, 2010) and compared the distributions of these

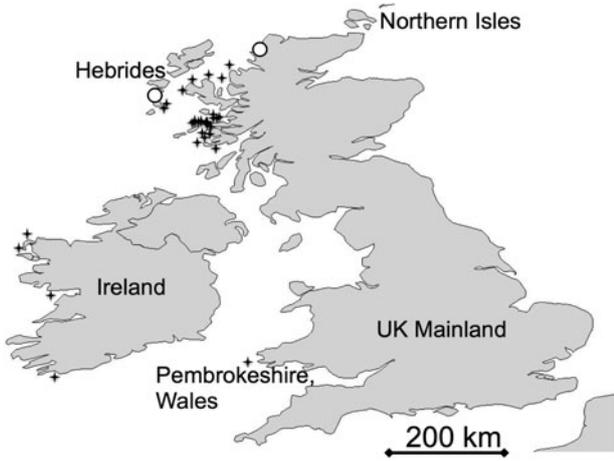


Fig. 2. A map of the British Isles and Republic of Ireland, showing the location of encounters from which high quality photographs allowing individual identification were collected. White circles indicate the locations of two recent stranded killer whales (see text for details).

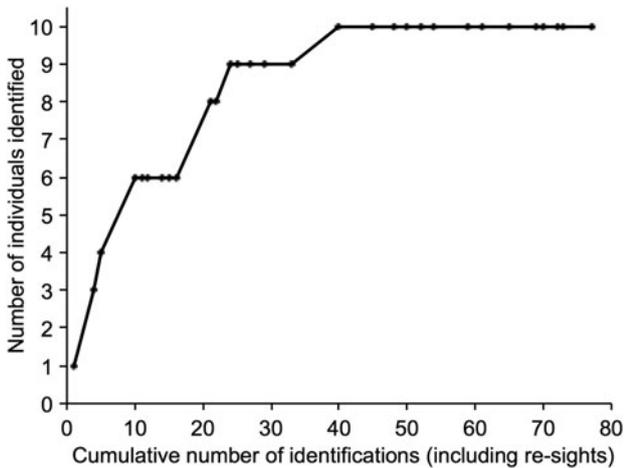


Fig. 3. Discovery curves showing the cumulative number of individuals identified with increasing effort indicated by the cumulative number of killer whales photo-identified (including re-sights) from encounters on 43 days between 1992 and 2011.

Table 1. Distinctiveness, re-sighting history and estimated age-class of identified individuals.

ID	M	1992	1995	1998	2000	2001	2004	2005	2007	2008	2009	2010	2011	Maturity when last sighted	Minimum age estimate
W01	2	X	X	X	X		X	X	X	X	X	X	X	Adult male	\wedge 35
W02	2	X	X	X	X		X	X	X	X	X	X	X	Adult male	\wedge 35
W03	2	X	X	X	X		X	X	X	X	X	X	X	Confirmed adult female	\wedge 30
W04	2	X	X	X	X		X	X	X	X	X	X	X	Adult male	\wedge 35
W05	1			X		X		X	X	X	X	X	X	Adult male	\wedge 30
W06	0			X			X	X	X	X	X	X	X	Adult female/sub-adult male	\wedge 15
W07	0			X			X	X	X	X	X	X	X	Confirmed adult female	\wedge 25
W08	0			X			X	X	X	X	X	X	X	Adult male	\wedge 25
W09	1						X	X	X	X	X	X	X	Adult female/sub-adult male	\wedge 10
W10	0						X	X	X	X	X	X	X	Adult female/sub-adult male	\wedge 10

discrepancy measures to estimate the exceeding tail area probability, termed the posterior predictive P -value.

To further investigate social structure within this population we conducted an analysis to estimate the strength of dyadic associations and identify preferred associates using SOCPROG 2.4 (Whitehead, 2009). The strength of association between dyads was measured using the simple ratio index, which generates a statistically unbiased estimate of association and is appropriate when association is defined by presence in the same group during a sampling period (Ginsberg & Young, 1992).

RESULTS

Photographs from 53 photographic encounters collected between 1992 and 2011, from the west coast of Scotland, Ireland and Wales (Figure 2) were analysed, and images were of sufficient quality for individuals to be positively

identified from 32 of these encounters. After just two encounters with high quality images all well-marked individuals ($M = 2$) had been photo-identified. After a further fifteen encounters with high-quality images, ten individuals had been photo-identified. No new individuals were identified in a subsequent 15 encounters, in which a cumulative total of 33 individuals were photo-identified, but were all re-sights (Figure 3), thus indicating that all or most of the individuals are now known.

During the study period, the community consisted of five adult males (Wo1, Wo2, Wo4, Wo5 and Wo8), two confirmed adult females (Wo3 and Wo7) based on having been first identified between 1992 and 1998 and not growing subsequent to those first encounters, and three individuals that could be adult females or sub-adult males (Wo6, Wo9 and Wo10), as the first photographs of these individuals were collected between 2005 and 2008 (Table 1). One individual (Wo4), an adult male, has not been photographed since 2001 and is the only identified individual that may have died during the study period (all other individuals were photo-identified in

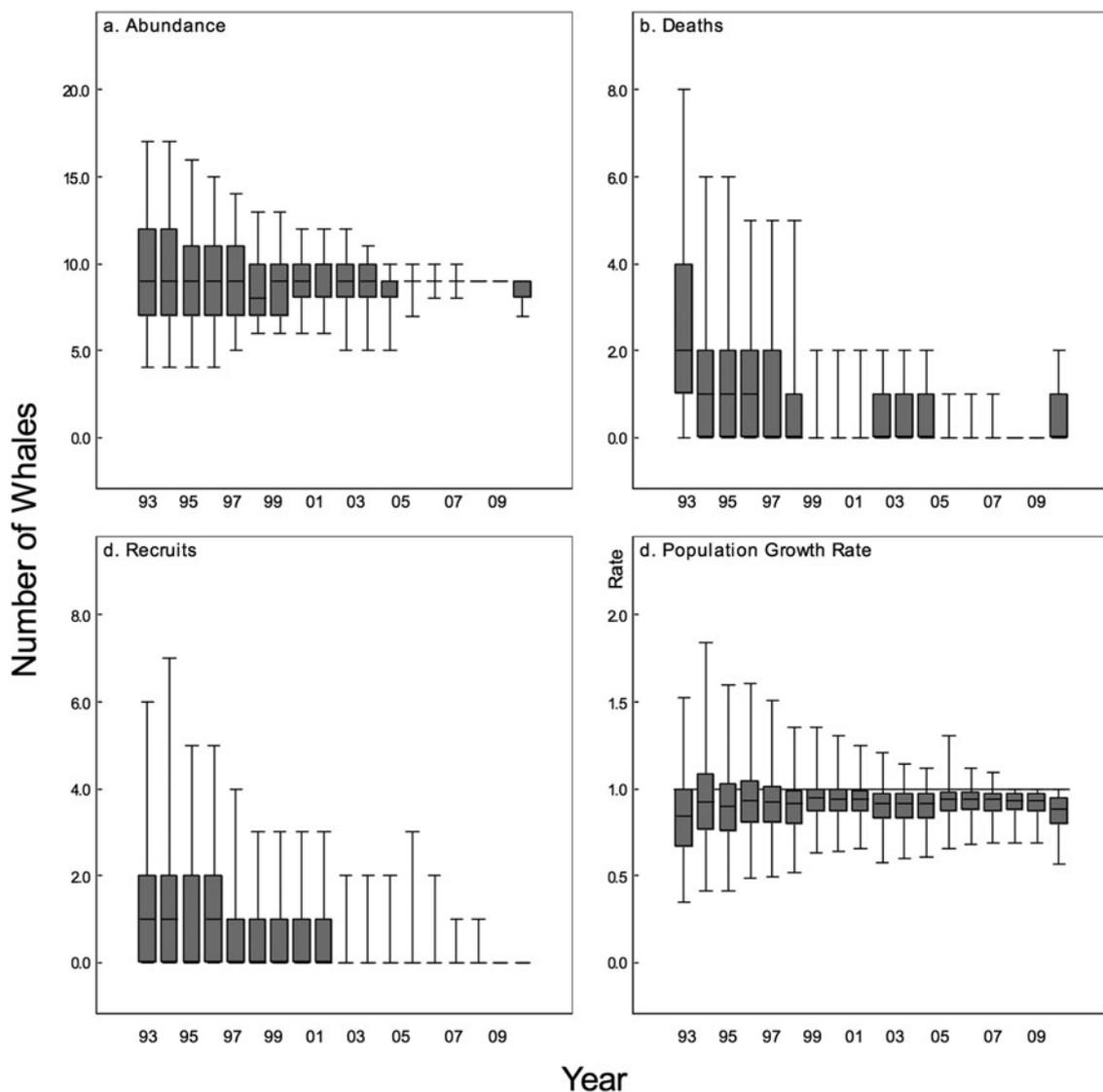


Fig. 4. Estimates of the abundance (N), number of deaths (D), recruits (R) and population growth rate (λ) for each year 1993–2010. Estimates from years 1992 and 1993 were omitted because capture probability was fixed in the model to ensure parameter identifiability (e.g. Fearnbach *et al.*, 2012). Vertical lines represent the full range of the posterior distribution for each parameter and boxes represent the 95% highest posterior density interval containing the posterior median (horizontal line).

2012). The remaining four adult males are estimated to be close to, or have surpassed, the mean life expectancy of 31 years found for Pacific resident killer whales (Olesiuk *et al.*, 1990; Table 1). No calves have been photographed in association with any of these individuals. The average inter-calf interval is approximately 6 years in other killer whale populations (Olesiuk *et al.*, 1990; Kuningas *et al.*, 2013). Two of the adult females (Wo3 and Wo7) were photographed as early as 1992 and 1998 and have been photographed at regular intervals (Table 1), and based on this average inter-calf interval would have been expected to have borne at least two calves each during this period if they were still reproductive.

The estimated probability of identification was low, with the medians of posterior probability distributions for the annual estimates averaging 0.3 (range of posterior medians = 0.07–0.75). However, the estimated identification probabilities were generally higher due to greater coverage in more recent years, providing increased power for estimating population dynamics towards the end of the time series. Despite greater uncertainty due to sparser observations at the start of the time series, estimates of abundance appear consistent across the time period (Figure 4A), with a most recent posterior median estimate of $N = 9$ whales (95% highest posterior density estimate (HPDI) = 7–9). Not unexpectedly, therefore, estimates of mortalities were low across the time series (Figure 4B), averaging less than one death per year, with a maximum posterior median estimate of only two deaths in any year (95% HPDI = 0–8), and 14 years with a posterior median of zero deaths. However, the number of recruits has also been low across the entire series (Figure 4C), with posterior median estimates of zero births in 16 of the years, and a maximum posterior median of just one birth in any year (95% HPDI = 0–7). As a result, there is evidence of a small population decline (Figure 4D), with the posterior median estimate for λ_t falling below one (population decline) for each year of the study. The probability of annual population decline was relatively high across the years (range = 0.66–0.99), with increasing probability in recent years ($P(\lambda_t < 1) > 0.9$ for the last six years of the study) when the posterior distribution for λ_t was more precise. Despite the sparse photo-identification data, there was good agreement between the discrepancy of observed and predicted data supporting that the model was a plausible

fit. The posterior predictive P -value equalled 0.62, indicating that the discrepancy of the data was similar (close to 0.5) to replications under the model (Gelman *et al.*, 1996).

A previous unweighted social network indicated that all individuals within this community are linked by association patterns and none have been seen in association with any other individuals (Foote *et al.*, 2010). The association index estimated here and presented as a dendrogram (Figure 5) shows there are clear preferred associates, and in each case this is an adult male and adult female (or putative adult female) pair.

DISCUSSION

The photo-identification data, although sparse and opportunistic, suggest that these ten photo-identified individuals form a small isolated population, which appears to be in a slight decline. Small population size and population declines can be due to high mortality, low fecundity or both. Studies on population dynamics in other declining killer whale populations have found that decreased survivorship across all age ranges is driving population trends, and have identified several common causes, including bioaccumulation of organic pollutants, prey depletion and lethal interactions with fisheries (Cañadas & de Stephanis, 2006; Matkin *et al.*, 2008, 2012; Ford *et al.*, 2010; Poncelet *et al.*, 2010). Potential threats to the killer whales on the west coast of Scotland include many of those listed above. However, whilst interpreting such sparse data as analysed in this study is difficult, it would appear that the apparent recent small decline is due to low recruitment, rather than higher than expected adult mortality. This apparent decline is, therefore, somewhat different to the patterns observed in other populations, and may suggest a different underlying driver.

The present small population size could result from historically higher mortality rates than at present, and the cause(s) may therefore have been historical. For example, 2435 North Atlantic killer whales were taken by Norwegian whalers between 1938 and 1981, including a small number from waters around North Scotland (Øien, 1988). Alternatively, one potential historical and non-anthropogenic cause of a low population size that would not require historical high mortality would be if the population resulted from a founder event by a single small group. There is some genetic evidence for a relatively recent founder event. Sequencing of the complete mitochondrial genome of two killer whales that stranded on the west coast of Scotland (Figure 2) indicated that they were very closely related to ‘type A’ killer whales sampled in Antarctic waters, and distantly related to other killer whales sampled around Scotland; that is, these lineages were relatively recent migrants to the North Atlantic (Foote *et al.*, 2011; Foote, unpublished data). These two stranded samples included a full-grown adult male in 2008 that was too decomposed to allow individual identification (however, the timing of the stranding does coincide with the cessation of sightings of Wo4) and a neonate in 2005. Therefore it was not possible to conclusively link these specimens to this community, and genetic samples are needed from the individuals photo-identified in this study to confirm that they belong to this ‘Antarctic’ lineage.

The unusual demography of this population, which consisted of 50% adult males, may indicate stochastic processes

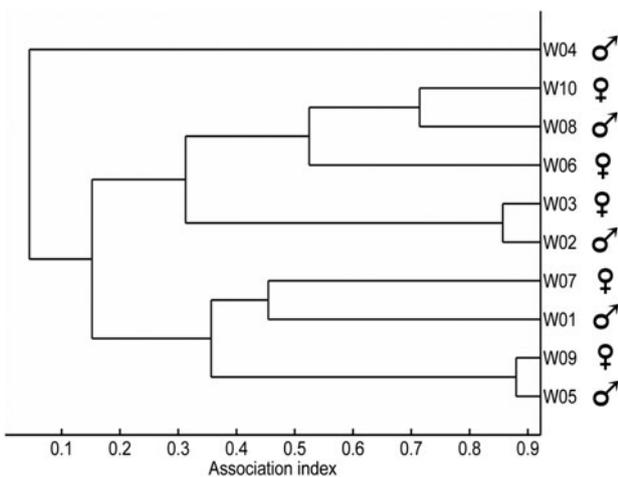


Fig. 5. Average-linkage cluster analysis of all individuals photo-identified and linked by association within this community.

due to the small population size are having an effect on recruitment. The population size may have reached a critical point whereby it experiences inverse density dependence or depensation (the 'Allee' effect) due to local factors, such as a loss of fitness from inbreeding, demographic stochasticity and reduced benefits of sociality (Courchamp *et al.*, 1999; Stephens & Sutherland, 1999; Jackson *et al.*, 2007; Wade *et al.*, 2012). If the strong male–female dyadic associations in this community represent mother–offspring relationships, as they do in other killer whale communities (e.g. Ford & Ellis, 1999; Ford *et al.*, 2000), it would suggest that most of these females are at, or are close to, an age where they would be expected to be post-reproductive (see Olesiuk *et al.*, 1990). Although inference of relationship based on association is an assumption, if true it would suggest that immigration into the community is necessary for it to survive beyond the lifespan of the existing members.

This study highlights the value of public involvement in widespread opportunistic sightings schemes, such as those operated by HWDT and IWDG, when studying highly mobile species with large home ranges and no obvious critical habitat or high sighting area to conduct dedicated fieldwork. The uncertainty associated with the analyses of the opportunistic photographic data decreased throughout the study, and in particular after 2005, when the number of individuals photo-identified annually increased. We suspect that this is due to the increase in the use of digital cameras around this time, which increased the quality of photographs, the number of photographs taken per encounter and the increased ease and reduced cost with which the public could forward photographs to the sightings networks. We therefore anticipate increasing use of opportunistically-collected photo-identification data and increasing value of this data for monitoring of populations.

In summary, the photo-identification data suggest that this population is isolated from neighbouring populations, is critically small (<10 individuals) and has a recent fecundity of zero. Therefore, we recommend recognition of this population as a discrete conservation management unit requiring that demographics and viability of this population be monitored independently rather than as part of the species as a whole in UK and Irish waters. Additionally, we recommend further direct research efforts to identify the current and historical threats that could have led to such a small population size, with biopsy sampling to facilitate genetic and contaminant analyses being a research priority.

ACKNOWLEDGEMENTS

We are particularly indebted to Karen Hall and Elaine Tait for their support of this project. Thanks to all members of the public, the local whale watching community and the crews of the SV 'Silurian' during this study that contributed towards the photo-identification dataset. An additional thank you to Rob Lott of Whale and Dolphin Conservation, (WDC) for reporting sightings from Pembrokeshire, Wales.

FINANCIAL SUPPORT

Funding for this research was provided by Marine Scotland and Scottish Natural Heritage.

REFERENCES

- Beck S., Kuningas S., Esteban R. and Foote A.D. (2012) The influence of ecology on sociality in the killer whale (*Orcinus orca*). *Behavioral Ecology* 23, 246–253.
- Brooks S.P. and Gelman A. (1998) General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics* 7, 434–455.
- Cañadas A. and de Stephanis R. (2006) Killer whale, or Orca *Orcinus orca* (Strait of Gibraltar subpopulation). In Reeves R.R. and Notarbartolo di Sciarra G. (eds) *The status and distribution of cetaceans in the Black Sea and Mediterranean Sea*. Malaga: IUCN Centre for Mediterranean Cooperation, pp. 34–38.
- Durban J., Ellifrit D., Dahlheim M., Waite J., Matkin C., Barrett-Lennard L., Ellis G., Pitman R., LeDuc R. and Wade P. (2010) Photographic mark-recapture analysis of clustered mammal-eating killer whales around the Aleutian Islands and Gulf of Alaska. *Marine Biology* 157, 1591–1604.
- Fearnbach H., Durban J.W., Parsons K.M. and Claridge D. (2012) Photographic mark-recapture analysis of local dynamics within an open population of dolphins. *Ecological Applications* 22, 1689–1700.
- Foote A.D., Newton J., Piertney S.B., Willerslev E. and Gilbert M.T.P. (2009) Ecological, morphological and genetic divergence of sympatric North Atlantic killer whale populations. *Molecular Ecology* 18, 5207–5217.
- Foote A.D., Similä T., Víkingsson G.A. and Stevick P.T. (2010) Movement, site fidelity and connectivity in a top marine predator, the killer whale. *Evolutionary Ecology* 24, 803–814.
- Foote A.D., Vilstrup J.T., Stephanis R. de, Verborgh P., Abel Nielsen S.C., Deaville R., Kleivane L., Martin V., Miller P.J.O., Øien N., Perez-Gil M., Rasmussen M., Reid R.J., Robertson K.M., Rogan E., Similä T., Tejedor M.L., Vester H., Víkingsson G.A., Willerslev E., Gilbert M.T.P. and Piertney S.B. (2011) Genetic differentiation among North Atlantic killer whale Q4 populations. *Molecular Ecology* 20, 629–641.
- Ford J.K.B. and Ellis G.M. (1999). *Transients: mammal-hunting killer whales of British Columbia, Washington, and southeastern Alaska*. Vancouver, BC: UBC Press.
- Ford J.K.B., Ellis G.M. and Balcomb K.C. (2000). *Killer whales, the natural history and genealogy of Orcinus orca in British Columbia and Washington*. Vancouver, BC: UBC Press.
- Ford J.K.B., Ellis G.M., Olesiuk P.F. and Balcomb K.C. (2010) Linking killer whale survival and prey abundance: food limitation in the ocean's apex predator? *Biology Letters* 6, 139–142.
- Gelman A., Meng X. and Stern H. (1996) Posterior predictive assessment of model fitness via realized discrepancies. *Statistica Sinica* 6, 733–759.
- Ginsberg J.R. and Young T.P. (1992) Measuring association between individuals or groups in behavioural studies. *Animal Behaviour* 44, 377–379.
- Joint Nature Conservation Committee (JNCC) (2007) *Second Report by the UK under Article 17 on the implementation of the Habitats Directive from January 2001 to December 2006*. Peterborough: JNCC. Available at: www.jncc.gov.uk/article17 (accessed 30 July 2013).
- Kuningas S., Similä T. and Hammond P.S. (2013) Population size, survival and reproductive rates of northern Norwegian killer whales (*Orcinus orca*) in 1986–2003. *Journal of the Marine Biological Association of the United Kingdom* 93.
- Law R.J., Allchin C.R., Jones B.R., Jepson P.D., Baker J.R. and Spurrier C.J.H. (1997) Metals and organochlorines in tissues of a Blainville's beaked whale (*Mesoplodon densirostris*) and a killer whale (*Orcinus orca*) stranded in the UK. *Marine Pollution Bulletin* 34, 208–212.

- Lunn D.J., Thomas A., Best N. and Spiegelhalter D.** (2000) WinBUGS – a Bayesian modelling framework: concepts, structure and extensibility. *Statistics and Computing* 10, 325–337.
- Luque P.L., Davis C.G., Reid D.G., Wang J. and Pierce G.J.** (2006) Opportunistic sightings of killer whales from Scottish pelagic trawlers fishing for mackerel and herring off North Scotland (UK) between 2000 and 2006. *Aquatic Living Resources* 19, 403–410.
- Matkin C.O., Durban J., Saulitis E.L., Andrews R.D., Straley J.M., Matkin D.R. and Ellis G.M.** (2012) Contrasting abundance and residency patterns of two sympatric populations of transient killer whales in the northern Gulf of Alaska. *Fishery Bulletin (US)* 110, 143–155.
- Matkin C.O., Saulitis E.L., Ellis G.M., Olesiuk P. and Rice S.D.** (2008) Ongoing population-level impacts on killer whales *Orcinus orca* following the ‘Exxon Valdez’ oil spill in Prince William Sound, Alaska. *Marine Ecology Progress Series* 356, 269–281.
- McHugh B., Law R.J., Allchin C.R., Rogan E., Murphy S., Foley M.B., Glynn D. and McGovern E.** (2007) Bioaccumulation and enantiomeric profiling of organochlorine pesticides and persistent organic pollutants in the killer whale (*Orcinus orca*) from British and Irish waters. *Marine Pollution Bulletin* 54, 1724–1731.
- Øien N.** (1988) The distribution of killer whales (*Orcinus orca*) in the North Atlantic based on Norwegian catches, 1938–1981, and incidental sightings, 1967–1987. *Rit Fiskideildar* 11, 65–78.
- Olesiuk P.F., Bigg M.A. and Ellis G.M.** (1990) Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Reports of the International Whaling Commission Special Issue* 12, 209–243.
- Poncelet É., Barbraud C. and Guinet C.** (2010) Population dynamics of killer whales (*Orcinus orca*) in the Crozet Archipelago, southern Indian Ocean: a mark-recapture study from 1977 to 2002. *Journal of Cetacean Research and Management* 11, 41–48.
- Royle J.A. and Dorazio R.M.** (2008) *Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities*. New York: Academic Press.
- Seber G.A.F.** (1982) *The estimation of animal abundance and related parameters*, 2nd edition London: Charles Griffin & Company.
- Sigurjónsson J. and Leatherwood S.** (1988) The Icelandic live-capture fishery for killer whales, 1976–1988. *Rit Fiskideildar* 11, 307–316.
- Similä T. and Lindblom L.** (1993) Persistence of natural markings on photographically identified killer whales (*Orcinus orca*). *International Council for the Exploration of the Sea. (CM papers and Reports)*, 1993/N: 11.
- Taylor B.L.** (1997) Defining ‘population’ to meet management objectives for marine mammals. In Dizon A.E., Chivers S.J. and Perrin W.F. (eds) *Molecular genetics of marine mammals. Special Publication 3*. Lawrence, KS: Allen Press, pp. 347–364.
- Wade P.R., Reeves R.R. and Mesnick S.L.** (2012) Social and behavioural factors in cetacean responses to overexploitation: are Odontocetes less ‘resilient’ than Mysticetes? *Journal of Marine Biology*. doi:10.1155/2012/567276.
- Whitehead H.** (2009) SOCPROG programs: analyzing animal social structures. *Behavioral Ecology and Sociobiology* 63, 765–778.
- and
- Wolkers H., Corkeron P.J., van Parijs S., Similä T. and van Bavel B.** (2007) Accumulation and transfer of contaminants in killer whales (*Orcinus orca*) from Norway: indications for contaminant metabolism. *Environmental Toxicology and Chemistry* 26, 1582–1590.
- Correspondence should be addressed to:**
O. Harries
Hebridean Whale and Dolphin Trust, 28 Main Street,
Tobermory, Isle of Mull, PA75 6NU, UK
email: biodiversityofficer@hwdt.org